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FEMALE NESTING BEHAVIOR AND MALE TERRITORIALITY IN *APHILANTHOPS SUBFRIGIDUS* DUNNING (HYMENOPTERA: SPHECIDAE)

KEVIN M. O'NEILL
Entomology Research Laboratory, Montana State University,
Bozeman, Montana 59717

Abstract.—The behavior of females and males of *Aphilanthops subfrigidus* Dunning was studied in southcentral Montana in 1987, 1988, and 1989. As with the related species *A. frigidus* (F. Smith), females of *A. subfrigidus* were found to specialize on alate queens of *Formica* (*F. subpolita* Mayr) that they capture at mating swarms of this ant. Several aspects of female nesting behavior are described, including their reaction to the presence of miltogrammine flies in the nesting area. In addition, male territoriality and scent-marking, which are widespread within the Philanthinae, are reported for the first time for this genus.

Key Words.—Insecta, *Aphilanthops, Formica subpolita,* nesting, territory

Aphilanthops is one of three North American genera of the sphecid subfamily Philanthinae with females that provision their nests with ants (Bohart & Menke 1976). Females of *Clypeadon* and *Listropygia* prey upon workers of *Pogonomyrmex* spp., with each wasp species apparently specializing on a single species of ant. Female *Aphilanthops frigidus* (Smith), restrict their prey to alate queens of *Formica* (Peckham & Peckham 1905, Wheeler 1913, Evans 1962). Several prey records obtained for *A. subfrigidus* Dunning suggest that it also specializes upon queens of *Formica* spp. (Evans 1970). In contrast, Evans (1977) reports bees as prey of *Aphilanthops hispidus* W. Fox, indicating that predation upon ants is not a consistent feature of this genus. Our knowledge of the behavior of female *Aphilanthops* is incomplete. Furthermore, of the five genera of Philanthinae that are relatively widespread in North America (*Aphilanthops, Cerceris, Clypeadon, Eucerceris,* and *Philanthus*), *Aphilanthops* is the only one for which male territoriality and scent-marking have not been reported (Evans & O'Neill 1988). We report observations of female nesting behavior and male territorial behavior in *A. subfrigidus.*

METHODS

Observations were made on *Aphilanthops subfrigidus* from 29 Jun–3 Jul 1987, 21 Jun–1 Jul 1988, and from 3–19 Jul 1989 at a site 13.5 km south of Three Forks, Gallatin Co., Montana. Male territories and female nest sites were located on the bottom and sides of several gullies, 0.5 to 1.5 km west of the Madison River. Over a three day period in 1987, five hours of focal observations were made on females at eight nests. Intermittent observations of both females and males were made at other times. The grassland site was within the *Stipa comata* Trinius & Ruprecht/*Bouteloua gracilis* (Humboldt, Bonpland, & Kunth) Lagasca y Segura ex. Steudel habitat type (Mueggler & Stewart 1980). Also present were three-leaf sumac (*Rhus trilobata* Nuttall), junipers (*Juniperus* spp.), and soapweed (*Yucca glauca* Nuttall).

Results and Discussion

Female Behavior.—In 1987, a nesting aggregation ultimately consisting of 11 nests within 4 m of one another, was discovered at the bottom of a gully 1 km west of the Madison River. While no nests were found at this location in 1988, a group of six nests was located in the same gully, approximately 100 m to the east. Only three other nests, each well-separated from other nests, were located during the three years of study. When present, the tumulus at each nest entrance was less than 1 cm in diameter. The absence of a substantial tumulus was also noted for *A. frigidus* (Evans 1962).

Eight of the nests were excavated, but the burrows were difficult to track, as was reported for *A. frigidus* (Peckham & Peckham 1905, Wheeler 1913, Evans 1962). All of the nests occurred in fine silt interspersed with small rocks and fine roots. The burrows entered the soil at angle of 30° to 45°. One burrow was followed for 24 cm to a depth of 23 cm. The main burrow of the nest doubled back upon itself, so the terminus was only 10 cm in horizontal distance from the entrance.

All prey found within nests were alate queens of *Formica subpolita* Mayr (Formicidae). Alate queens of *Formica neogates* Emery were reported as prey of *A. subfrigidus* from a single nest excavated in Jackson Hole, Wyoming (Evans 1970). Two nest cells containing three and four prey were found at depths of 15 and 20 cm, each at a distance of 1 cm from the main burrow. Twelve additional prey were found stored in the main burrows of four other nests (one to seven per nest), all within 10 cm of the entrance. All seven prey found in the nest cells and two of those found in burrows lacked wings. The wings of all but one of these prey had apparently been chewed off by the provisioning female, rather than shed because the fragmented bases of the wings were present. Ten of 12 ants found in the burrows had wings.

At least some of the prey were captured at mating swarms of *F. subpolita,* several of which were within 3 m of the 1988 nest site. *A. subfrigidus* were observed at the mating swarms 13 times. Successful capture of an alate female at swarms was observed once; three other females were seen leaving swarms carrying prey. The female *A. subfrigidus* themselves were taken a prey by the robber fly *Efferia staminea* (Williston) (Asilidae) near the ant swarms ($n = 4$).

Females began bringing prey into nests shortly after 09:00 h RMST and continued foraging until between 10:17 and 11:05 h. This overlapped with the period during which mating swarms of *F. subpolita* were observed on *Rhus trilobata* on 11 days in June and July, 1988 and 1989 (unpublished data). Seasonal synchrony between predator and prey species was also observed. The first sightings of *A. subfrigidus* in 1988 and 1989 occurred one and four days, respectively, after swarms of the ants first appeared.

Storage of prey in the burrow allowed females to spend very little time in the nest during the short daily period available for hunting. They spent 0.5 to 3.6 min ($\bar{x} = 1.8$, $n = 23$) inside the nest between foraging flights 2.2 to 9.8 in duration ($\bar{x} = 5.2$, $n = 20$). During a 1 h observation period, three females brought 5, 6, and 11 prey to their nests. Thus, if three or four prey per cell is typical for this species, females were obtaining prey for more than a single cell in a morning. This would seem advantageous because the mating swarms of *Formica* occurred for only several hours per day, on only 11 of the 17 days on which *A. subfrigidus* was

observed in 1988 and 1989. Winged females were only rarely observed on days on which swarms did not take place.

The nest entrance was left open by the females during 86% of the foraging flights observed ($n = 37$). However, seven females returning to nests after the final daily foraging flight and five leaving the nests for prolonged non-foraging periods all closed the nest with a loose plug of soil. Facultative temporary nest closures have also observed in *A. subfrigidus* (Evans 1962) and in several species of *Philanthus* (Evans & O'Neill 1988) and are thought to prevent entrance by cleptoparasites. One final nest closure was observed. Over a period of 30 min, the female plugged the top three cm of the burrow with soil before initiating a second nest two m away.

Females approaching nests carrying prey sometimes behaved differently when being pursued by cleptoparasitic *Senotainia* spp. (Sarcophagidae). In 22 of 32 return flights, the females with prey were not followed by the miltogrammine flies. These 22 flew to the nest and either entered directly, or after dropping the prey at the entrance, entered, turned, and pulled in the prey. However, of the 10 flights observed when females were pursued by one ($n = 5$) or two ($n = 5$) flies, five females continued their approach and entered the nest, whereas the other five turned in flight and left the area. This apparently evasive action was observed in *A. frigidus* (Wheeler 1913) and in many species of *Philanthus* (Evans & O'Neill 1988). Ristich (1956) and Evans (1962) found high levels of miltogrammine parasitism in *A. frigidus*.

Male Behavior.—Groups of males were found in four locations from 21–29 Jun 1988 where they perched 1–2 m high on *Rhus trilobata* in three areas and on grasses growing adjacent to *Yucca* in another. The types of behavior displayed by males were generally identical to those of many other Philanthinae (Evans & O'Neill 1988). From perches 0.5–2 m high, males pursued passing insects and engaged in interactions with conspecific males. These interactions included: (1) "swirling flights" when two to four males rapidly and repeatedly circled one another in flight within a radius of less than 10 cm; (2) "butting" when males made brief, but forceful and often repeated head-on contact in mid-air; and (3) "grappling" when males grasped one another in mid-air and sometimes fell to the surface below where they continued wrestling for several seconds. All three of these behaviors have also been observed in the related genus *Philanthus*. In that genus, specific butting and grappling episodes are sometimes best interpreted as misdirected mating attempts. However, in *Philanthus,* interactions among males often differ markedly from male–female encounters. They occur repeatedly between two males over short intervals and commonly result in the perch occupant being driven from the area and replaced by the intruder. Thus, in *Philanthus* and, probably *Aphilanthops* as well, these behaviors, especially repeated bouts of butting and grappling, represent aggressive interactions associated with territorial defense and exclusive occupation of areas immediately surrounding perches (Evans & O'Neill 1988).

At three of the four aggregations, 7–14 territories were found. All territories in each aggregation were within 5–20 m of one another, with perches of adjacent males often less than a meter apart. Because the number of males at an aggregation was at least twice the number of territories, interactions were common.

Territorial males also exhibited "abdomen dragging," another behavior typical

of male philanthines. Males walked up the stems of grasses with the hair brushes of their clypeal area and posterior venter of their abdomen in contact with the plant. On *Rhus,* they walked along the edges of the leaves. This behavior probably serves to deposit a pheromone that attracts females (Evans & O'Neill 1988). Schmidt et al. (1985) found that male *Philanthus basilaris* deposited volatile substances onto plant from their mandibular glands while abdomen dragging. The clypeal hair brushes of male *Aphilanthops* are shorter and less dense than those of male *Philanthus.* The abdominal hair brushes are also sparser, although distinct rows of short hairs ("fimbriae") are present on abdominal sterna IV and V (Bohart & Grissell 1975).

The territorial areas lacked flowering plants or honeydew sites likely to attract conspecific females and although nests were nearby, nests did not occur in the large aggregations sometimes found in philanthines (Evans & O'Neill 1988). Other nests were scattered throughout the area that contained territories. Although territories of males at two of the areas were within swarms of *Formica subpolita,* the latter were not observed at the other two territorial areas.

The behavior of female *A. subfrigidus* is similar to that of *A. frigidus* (Peckham & Peckham 1905, Wheeler 1913, Evans 1962), particularly with regards to prey use. Comparative data from other philanthines suggest the interactions observed among male *A. subfrigidus* result from attempts of males to exclude conspecific males from areas containing scent-marked plants. Although territoriality has been reported in many Sphecidae, scent-marking of territories has been observed only within five genera of the Philanthinae (Evans & O'Neill 1988). The presence of the clypeal hair brushes in four of the six remaining undocumented genera (Bohart & Menke 1976) suggests that territoriality and scent-marking maybe even more widespread within the subfamily.

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